PHYSIOLOGICAL AND MORPHOLOGICAL ADAPTATIONS OF ADULT *UCA SUBCYLINDRICA* TO SEMI-ARID ENVIRONMENTS[1]

NANCY N. RABALAIS[2] AND JAMES N. CAMERON

The University of Texas at Austin, Port Aransas Marine Laboratory, Port Aransas, Texas 78373

ABSTRACT

Salinity tolerance, osmotic and ionic regulation abilities, desiccation tolerance, and gill morphometry of *Uca subcylindrica,* which inhabits semi-arid supratidal areas, were compared with more typically intertidal fiddler crabs, especially *U. longisignalis.* Salinity tolerance was less in *U. subcylindrica* (2–90‰) than in *U. longisignalis* (0.08–110‰). Blood osmolality and sodium and chloride concentrations were regulated over a wide range of salinities in both species, but *U. subcylindrica* maintained a smaller gradient against the external medium at the lowest salinity at which it survived and at the higher salinities. The osmoregulatory responses were contrary to predictions based on field distributions, but *U. subcylindrica* generally survived desiccation longer and always tolerated a greater percent body water loss than *U. longisignalis, U. rapax,* and *U. panacea.* Differences in gill morphometrics among the four species were consistent with features accompanying increasing terrestriality.

INTRODUCTION

In the western Gulf of Mexico, several species of the typically intertidal genus *Uca* occur, including *U. longisignalis, U. rapax,* and *U. panacea* (Crane, 1975; Barnwell and Thurman, 1984). These crabs inhabit coastal marshes, intertidal areas bordering bays, lagoons and tidal creeks, and the periphery of wind tidal flats. One species, however, *U. subcylindrica,* inhabits areas distinctly different from the others (Rabalais, 1983; Thurman, 1984). This species is restricted to semi-arid habitats from Copano Bay, Texas to Tampico, Mexico. *Uca subcylindrica* lives in supratidal areas removed from permanent bodies of water and also occurs along intermittent stream courses and near ephemeral ponds up to 35 km from tidewater. Other species of *Uca* seldom occur in the habitats of *U. subcylindrica.*

Due to the low rainfall, limited tidal exchange with marine waters, and generally high temperatures and evaporation rates in this region, habitat conditions for *Uca subcylindrica* often include high salinity in the available water (up to 90‰; Rabalais, 1983), lack of standing water for extensive periods, and highly variable and extreme salinities in both standing water and burrow water, due to the periodically heavy rainfall. Salinity conditions for other fiddler crabs are more moderate: *e.g., U. longisignalis* occupies habitats with burrow water or adjacent bay waters ranging from 18 to 34.5‰ (Rabalais, 1983).

Physiological responses to salinity and drying conditions are important in the distributions and differential habitat selection of other decapod crustaceans (*e.g.,* Teal, 1958; Barnes, 1967; Engel, 1977; Felder, 1978; Young, 1978, 1979). The purpose of

the present investigation was to assess the responses of *Uca subcylindrica* to various stresses associated with their peculiar habitat, to compare these responses with other *Uca* species of the region, and to compare the morphometry of the gills among *Uca* species of varying degrees of terrestriality.

MATERIALS AND METHODS

Collection and maintenance of animals

Uca subcylindrica were collected from two main sites: an intermittent fresh to hypersaline creek (Santa Gertrudis Creek near Kingsville, Texas) and an ephemeral pond near the junction of the Laguna Madre and Baffin Bay, Texas. Individuals from the two areas did not differ in salinity tolerance, percent body water, and blood osmotic and ionic parameters across a salinity range of 2 to 90‰ (Rabalais, 1983), and were combined for comparison with the other species. Specimens of *U. longisignalis*, *U. rapax*, and *U. panacea* were collected from various salt marsh and intertidal habitats of the Corpus Christi, Nueces, and Aransas Bay systems.

Crabs were maintained in large circular tanks with natural sediment and water of about 30‰ salinity available. Feeding was halted 3 days prior to experiments, except in the osmoregulation experiments, in which food was given every 5 days during the 45-day experimental period. Only adult (≥12 mm, carapace width) intermolt males and non-ovigerous females were used; most were 15 to 20 mm.

Osmotic and ionic regulation

Crabs were kept in large fingerbowls with 2 cm of water which allowed access to air but kept the animals partly submerged. Animals were maintained at $22 \pm 1°C$ under a 14L:10D photoperiod and initially acclimated to 30‰. Other salinities were prepared either by dilution of natural sea water with deionized water or by concentration with artificial sea salts (Instant Ocean). An artificial pond water (0.5 mM NaCl, 0.4 mM CaCl$_2$, 0.2 mM NaHCO$_3$, and 0.05 mM KCl) gave the lowest physiologically meaningful salinity of 0.08‰.

The time required for adjustment to salinity change was determined in a preliminary experiment with three groups of five *Uca subcylindrica*. After 7 days at 30‰, one group was transferred to 10‰, another to 60‰, and the third left at 30‰. Blood osmolality values at 0.5, 1, 2, 3, 5, and 7 days showed that although there were some (non-significant) fluctuations in the first 3 days, there were no significant changes after 5 days. Blood parameters of crabs held 9 days at 2 and 80‰ did not differ significantly from those held 5 days. Thus, an acclimation period of five days was considered sufficient at all salinities and was used in all further salinity acclimation experiments.

The long-term salinity experiments with *Uca subcylindrica* and *U. longisignalis* were conducted as follows: for each species an initial group was acclimated for 5 days at 30‰ after which 5 individuals were sampled. Then half of the group was moved to a higher salinity, and half to a lower, left 5 further days, sampled, and moved again until either the entire range of 0.08 to 120‰ was covered or no more crabs survived. The salinity was monitored daily, readjusted as necessary, and the water changed every two days.

Blood samples were removed with a syringe from the arthrodial membrane at the base of the fifth pereiopod, allowed to clot, centrifuged, and refrigerated until analyzed, usually within 4 to 48 h. Osmolality of blood and water samples was determined on a vapor pressure osmometer (Wescor), chloride concentrations with

an amperometric titrator (Buchler-Cotlove), and sodium by flame photometry (Radiometer).

For field comparison, water samples were aspirated from burrows through flexible plastic tubing. Crabs, blood samples, and water samples were placed on ice until returned to the laboratory for processing as described above.

Desiccation tolerance

Crabs held for 3 days in water of 30‰ were blotted dry, weighed, and placed in individual ventilated plastic vials in a desiccator containing 250 g of dried $CaSO_4$, which produces a relative humidity of 0 to 10% (Jones and Greenwood, 1982). Blood osmolality of a few individuals not desiccated was measured at the beginning as a control. Vials were weighed at 4-h intervals until animals began to die, then hourly observations were made. All crabs were weighed on the same schedule so that manipulations and exposure to room air were consistent. Laboratory conditions were $22 \pm 15°C$ and 24-h dark.

Death was defined as lack of responsiveness to probing of antennae or appendages. At death, the final weight and blood osmolality were determined. The percent water loss was expressed as the loss in weight (assumed to be all water loss) as a percentage of initial weight of body water.

Gill morphometry

Gills from crabs held 1 week at 30‰ were preserved in either 10% buffered formalin or 0.1 M Na cacodylate buffer. Those used for examination of thick and thin epithelium were post-fixed in 1% OsO_4 for 2 h (Copeland and Fitzjarrell, 1968). Some of the gills were also paraffin embedded and sectioned for measurement of thickness of epithelia.

To avoid size-related differences, similar-sized crabs were used. Because the gills were generally subquadrate, they were cut into three sections—a small distal end, a small proximal end, and a large middle section that was visibly about the same circumference for its length. A representative platelet was cut from each section, the area determined, and the number of platelets per section counted, allowing the calculation of gill area by:

$$\sum_{i=1}^{6} [(D_i \cdot a \cdot 2) + (M_i \cdot a \cdot 2) + (P_i \cdot a \cdot 2)] \cdot 2;$$

where, D, M, and P = number of platelets in distal, middle, and proximal sections; a = area of a representative platelet from each; and i = the number of the gill pair. The percentage of thick epithelia was determined from *camera lucida* drawings of representative platelets with an integrating planimeter.

RESULTS

The highest and lowest tolerated salinities, those in which 50% survived 5 days, were 2 and 90‰ for *Uca subcylindrica* (Fig. 1). The highest tolerated salinity for *U. longisignalis* was 110‰; there was 100% survival in the lowest tested salinity of 0.08‰ (Fig. 1). Increased mortalities at the extremes could be attributed to these conditions, because high survival (>90%) occurred in 30‰ for longer than the 25 days when survival began to decrease in the long-term salinity experiments.

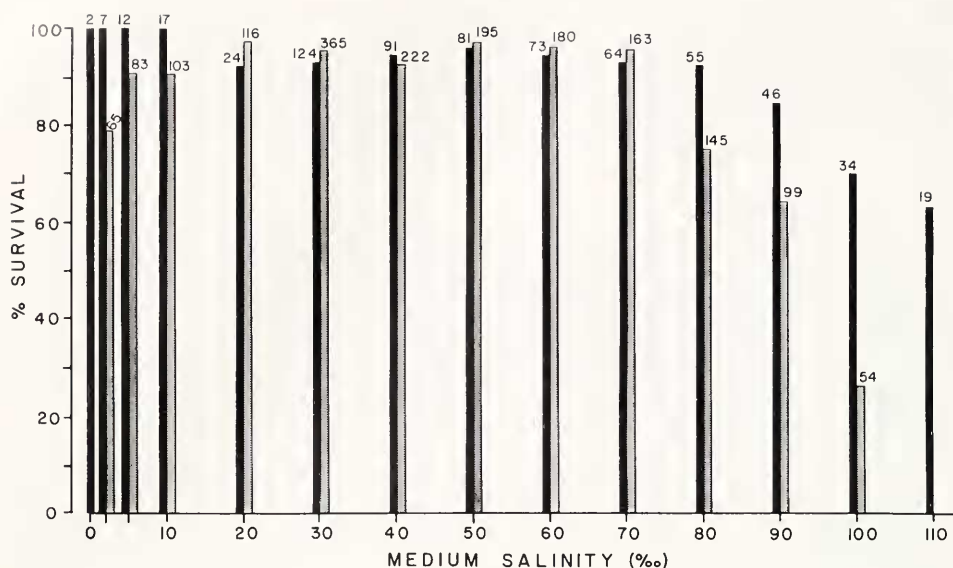Blood osmolality, as well as the principal ions Na^+ and Cl^-, were well regulated

FIGURE 1.   Percent survival of *Uca subcylindrica* in a range of salinities from 2 to 100‰ (shaded histograms) and *U. longisignalis* across a range of salinities from 0.08 to 110‰ (dark histograms). n for each group given above histograms.

over a wide range of salinities in both species (Fig. 2). The isosmotic and isoionic points were higher in *U. subcylindrica*. *Uca subcylindrica* maintained less of a gradient against the external media at the lowest salinity (2‰) in which it survived and at the higher salinities (40‰ to the limits of survival) than *U. longisignalis* (*t*-Test, $P \leq 0.05$). Blood parameters for *U. subcylindrica* were more variable than those for *U. longisignalis*. The average percent body water of *U. subcylindrica* at all salinities was slightly greater than *U. longisignalis* (65.1 ± 0.4% *versus* 63.1 ± 0.4%), but values were not consistently greater across the range of salinities and usually not significantly different within a salinity.

In the field, *Uca subcylindrica* also regulated effectively, with blood osmolality staying within narrow limits in the presence of water of widely varying salinity (Fig. 3). The [Na^+] and [Cl^-] data (not shown) reflected a similar pattern with [Na^+] values generally between 370 and 450 mEq/l and [Cl^-] values between 280 and 350 mEq/l. Total body water for field-collected animals ranged from 55 to 65%, not significantly different from laboratory-acclimated animals.

Desiccation tolerance

Despite an effort to collect similar-sized crabs, the average carapace width differed significantly among the species (*t*-Tests, $P \leq 0.05$) (Fig. 4). Initial weights of *Uca panacea* and *U. subcylindrica* also differed from each other and from the other two species which were similar. Initial percent body water was not significantly different among species. Initial blood osmolality was similar in all species except *U. longisignalis*. With all values pooled, *U. subcylindrica* survived longer than *U. longisignalis* and *U. panacea* but not longer than *U. rapax* (Fig. 4). *Uca subcylindrica* withstood a greater percent body water loss than did the others which is reflected in lower final percent body water and higher final blood osmolality (Fig. 4). Final percent body

water did not differ significantly but final blood osmolality values did. The difference in initial and final blood osmolality was also much greater for *U. subcylindrica* (558 mOsm/kg) than for *U. longisignalis* (295 mOsm/kg), *U. rapax* (395 mOsm/kg), and *U. panacea* (309 mOsm/kg).

There were weak but significant ($P \leq 0.05$) linear relationships between size (as indicated by carapace width and initial body weight) and survival time in *Uca subcylindrica*, *U. longisignalis*, and *U. panacea* but not in *U. rapax*. Percent water loss was not correlated to size for any species. Thus, groups of similar-sized crabs were compared (Fig. 5A, B). In Group A, survival time was longer for *U. subcylindrica* but only significantly longer than *U. longisignalis* (*t*-Tests, $P \leq 0.05$). Within Group A, *U. subcylindrica* withstood a significantly greater percent body water loss. For Group B, *U. subcylindrica* survived significantly longer and withstood a significantly greater percent body water loss. There were no sex-related differences in survival time, but there were in percent water loss in *U. longisignalis* and *U. panacea* (Table I). Comparisons among the same sexes of similar-sized crabs showed that survival time was greater for *U. subcylindrica* but not always significantly and that percent body water loss was always significantly higher for *U. subcylindrica* (Fig. 5C, D).

Gill morphometry

Gills of *Uca* were morphologically similar to other terrestrial crabs (*e.g., Holthuisana transversa* in Taylor and Greenaway, 1979; *Cardisoma carnifex* in Cameron, 1981) with stiffened platelet margins for structural support, wide interlamellar spacing, and cuticular spines at the base of the efferent blood vessels. There were no obvious morphological differences among the gills of the different species. Gills 1 and 2 contributed little to the total gill surface area with gills 3–6 contributing the bulk (Table II). On the average, 81% of the epithelium was of the thick type (Table II) and averaged 5.2 μm thickness compared to 2.6 μm for the thinner type.

Total platelets, total gill surface area, and gill surface area per wet weight of crab were least in *U. subcylindrica* and varied significantly among the species (Table III). Separation of the data by sex, or expression of area per unit dry weight, ash-free dry weight, or weight minus a major cheliped did not add any significant insights.

DISCUSSION

Osmotic and ionic regulation

Several studies have shown *Uca* to accommodate to a wide salinity range by maintaining fairly uniform ionic and osmotic blood levels. Green *et al.* (1959) showed no significant differences in osmoregulation in *U. rapax* and *U. pugilator*, and both species were intermixed in studies by Baldwin and Kirschner (1976a, b). Wright *et al.* (1984) found no major differences in ionic regulation among *U. pugnax*, *U. pugilator*, and *U. minax*. Studies of other decapod crustaceans (Engel, 1977; Felder, 1978; Young, 1979), however, have shown that osmotic and ionic regulatory abilities of closely related species differ and correlate with their distributions in habitats of differing salinities. Based on the more extreme salinities in the habitats of *U. subcylindrica*, we expected to find a greater salinity tolerance and greater osmotic and ionic regulatory ability in these crabs. Even though the osmoregulatory ability of *U. subcylindrica* is considerable, it is not greater than that of *U. longisignalis* in long-term salinity experiments, and, in fact, is less (Figs. 1, 2).

The field data for *Uca subcylindrica* (Fig. 3; Rabalais, 1983) indicate that this species was a nearly perfect regulator in the face of an almost 10-fold variation in
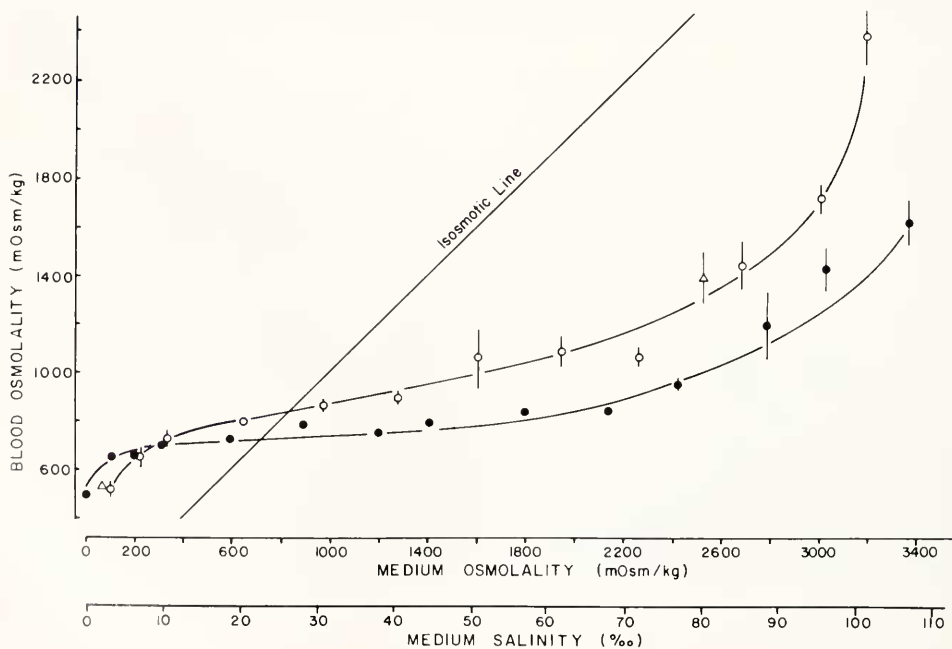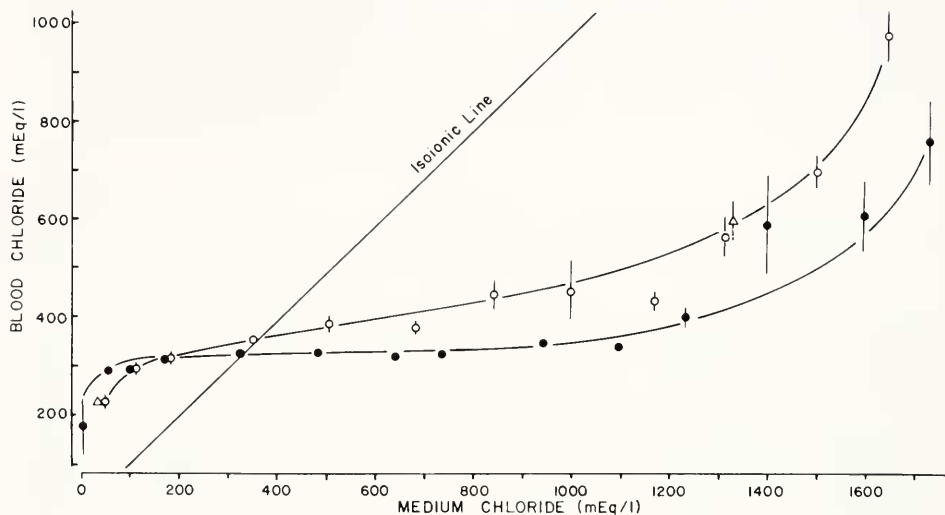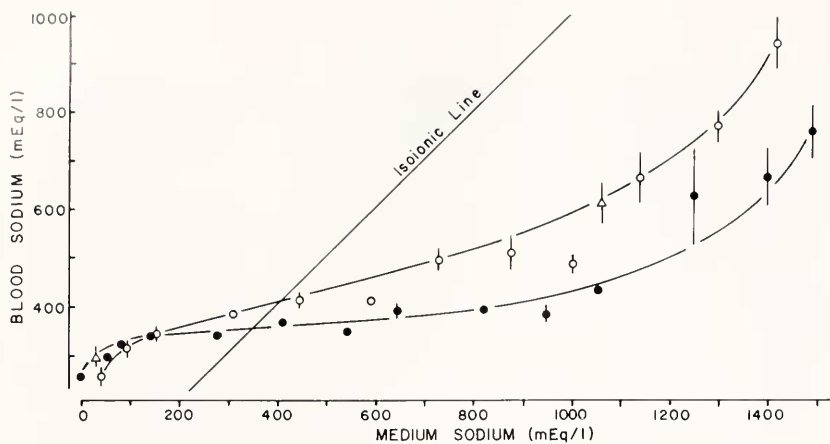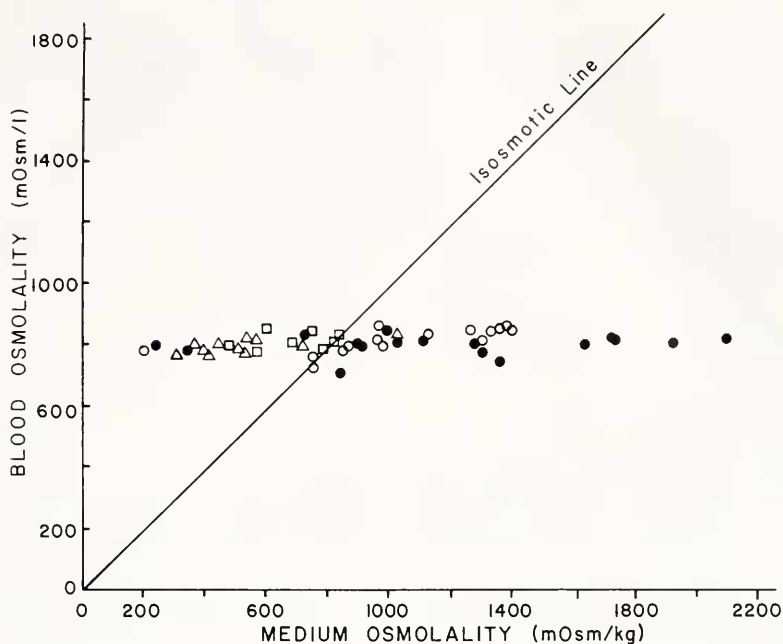
FIGURE 3. Blood osmolality values for *Uca subcylindrica* collected from burrows in the field as a function of the burrow water osmolality. Closed circles represent individuals collected 28 April 1981 from the Laguna Madre area; open circles, 28 May 1981 from the Laguna Madre area; squares, 14 July 1981 from Santa Gertrudis Creek; and triangles, 2 November 1982 from Santa Gertrudis Creek.

the osmolality of available water. This suggests that additional factors, such as behavioral osmoregulation involving selective drinking, may be important. Whether *U. subcylindrica* is more adept in this respect than other fiddler crabs is not known.

Desiccation tolerance

Crabs as a group can tolerate significant water loss, varying from 20 to 50% depending on species (reviewed by Jones and Greenwood, 1982). The 29% average for *Uca subcylindrica* reported here is not particularly remarkable, although it is greater than the other *Uca* examined. Young (1978) argued that the percent water loss tolerated was a good unbiased measure of desiccation tolerance, but found more significant interspecies differences based on survival time. In our study, differences in survival time were not as great among the species as the differences in water loss values (Figs. 4, 5).

Given the limited differences in size and initial blood osmolality values but no differences in percent body water and no chance for behavioral modification, the

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FIGURE 2. Blood osmolality, chloride, and sodium values for *Uca longisignalis* (closed circles) and for *U. subcyclindrica* (open circles) as a function of media osmolality, chloride, and sodium. Values represent the means of 5 determinations ±S.E. for *U. longisignalis* and 10 determinations ±S.E. for *U. subcylindrica*. Triangles represent groups of *U. subcylindrica* acclimated for nine days as opposed to five days for the others. Approximate salinity values given on a second abscissa below osmolality (lowest values at 0.08‰); data plotted against osmolality and ionic concentrations. Curves fitted by eye.
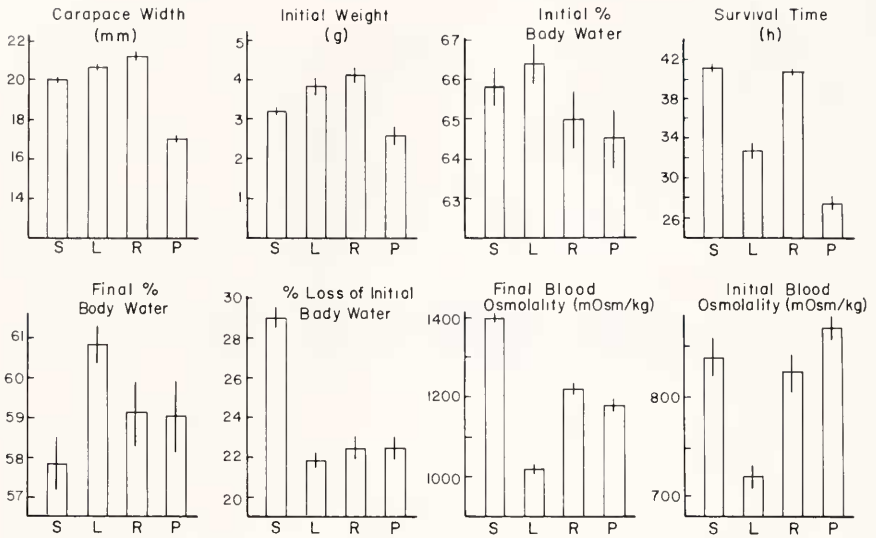
FIGURE 4.   Comparison of several parameters in desiccation tolerance experiments for four species of fiddler crabs: S = *Uca subcylindrica*, n = 114; L = *U. longisignalis*, n = 79; R = *U. rapax*, n = 26; and P = *U. panacea*, n = 55. For initial blood osmolality, n = 17 for S, n = 14 for L, n = 5 for R, and n = 13 for P. Vertical lines represent ±S.E.
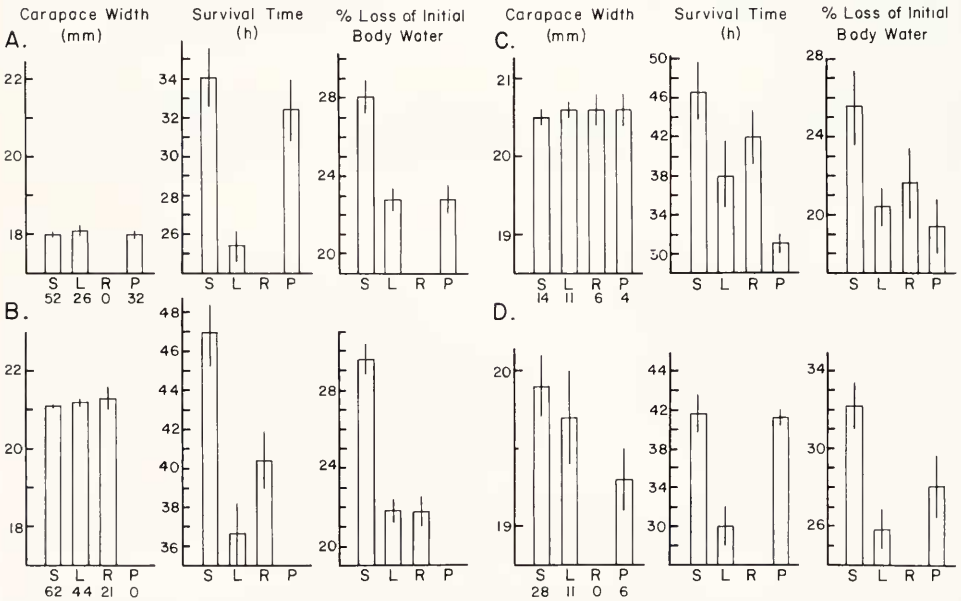

FIGURE 5.   Comparison of carapace width, survival time, and percent loss of initial body water in desiccation tolerance experiments for four species of fiddler crabs, grouped by size and sex. Group A is 15.3–19.9 mm, carapace width, males and females; B is 20.0–23.7 mm, carapace width, males and females; C is 20.1–21.3 mm, carapace width, males; D is 18.0–20.1 mm, carapace width, females. S = *Uca subcylindrica*, L = *U. longisignalis*, R = *U. rapax*, and P = *U. panacea*. n for each species in each group given below designation in carapace width data set. Vertical lines represent ±S.E.

TABLE I

Comparison of desiccation tolerance data (survival time and percent loss of initial body water) between similar-sized male and female crabs of three species of fiddler crabs.

Species and sex	Carapace width (mm)	Survival time (h)	% Loss of initial body water
Uca subcylindrica			
Males	18.9 ± 0.2	39.6 ± 4.3	24.7 ± 1.1
Females	18.9 ± 0.2	35.1 ± 3.1	29.5 ± 2.6
t-value	−0.8944	0.7080	−1.8380
Uca longisignalis			
Males	19.5 ± 0.3	25.9 ± 1.3	19.6 ± 1.2
Females	19.5 ± 0.3	28.5 ± 1.8	26.2 ± 0.4
t-value	0.7559	−1.3420	−5.6726*
Uca panacea			
Males	18.7 ± 0.3	33.1 ± 2.2	20.0 ± 0.7
Females	18.7 ± 0.3	36.2 ± 2.7	26.5 ± 1.3
t-value	0.1440	−0.9523	−4.3857*

Values of the *t*-distribution marked with an * are significant ($P \leq 0.05$, for df = 10).

differences in desiccation tolerance indicate varying physiological abilities among the species and should provide an index of the ability to survive such conditions in the field. In that way, the laboratory data on *Uca subcylindrica* do correlate with the known field distributions and habitat conditions.

The ability of *Uca subcylindrica* to tolerate desiccation better may be related to reduced permeability, reduced surface areas, or an ability to lose sufficient water from the blood or tissues across gill surfaces to maintain a relative humidity in the branchial chamber necessary for respiration. A reduced gill surface area (Table III) would reduce the loss of water by transpiration. The increased blood osmolality was probably not a factor based on known comparative salinity tolerances and osmoregulatory abilities of *U. subcylindrica* and *U. longisignalis* (Figs. 1, 2).

In the field, behavioral mechanisms not possible in laboratory experiments may importantly compensate for desiccating conditions. Activity peaks around dawn in the warmer months (pers. obs.) may be related to the crabs' use of dew which has condensed on sediments and plants. These activity patterns, however, may as likely

TABLE II

Distribution of gill area by individual gill pair and by epithelium type for Uca subcylindrica *and* U. longisignalis

Gill pair (anterior to posterior)	*Uca subcylindrica*		*Uca longisignalis*	
	% of total area	% thick epithelia	% of total area	% thick epithelia
1	1.9 ± 0.1	87.8	1.7 ± 0	81.6
2	2.5 ± 0.6	80.2	1.0 ± 0.1	88.6
3	17.8 ± 0.8	80.0	19.5 ± 1.6	80.7
4	39.0 ± 1.0	79.4	30.7 ± 0.5	81.7
5	22.0 ± 0.4	77.9	26.1 ± 1.2	79.5
6	16.9 ± 0.7	83.7	20.9 ± 1.2	80.4

Values are means ± S.E.

Comparison of gill morphometry for four species of Uca

Species	Carapace width (mm)	Wet weight (g)	Total platelets	Total gill surface (mm²)	Gill area/ wet weight (mm²/g)
Uca longisignalis (6)	21.3 ± 0.7	3.9 ± 0.9	926 ± 17	2237 ± 181	658 ± 78
Uca rapax (1)	21.1	2.9	846	1751	595
Uca panacea (3)	19.6 ± 0.3	2.8 ± 0.1	775 ± 18	1575 ± 142	566 ± 44
Uca subcylindrica (8)	20.7 ± 0.5	3.5 ± 0.2	698 ± 8	1482 ± 78	432 ± 19
F-value, df = 2, 14	1.3207 NS	0.6405 NS	89.7118 ***	10.0912 ***	5.8385 *

Values are means ± S.E.; n for each group given in parentheses following species designation. NS: not significant, $P > 0.05$; *: $0.01 < P \leq 0.05$; ***: $P \leq 0.001$.

be related to avoidance of hotter temperatures during mid day and predators at night. *Uca subcylindrica* may also utilize water from plants brought into their burrows, *e.g.*, *Batis, Sueda,* and *Borrichia* (pers. obs.).

Gill morphometry

The reduced gill area in *Uca subcylindrica* is no doubt related to the lesser requirement for gas exchange area in terrestrial crabs (Cameron, 1981) but may also play a role in reducing evaporative water loss in arid environments. Comparisons of gill area have been made for widely disparate groups (*e.g.*, Pearse, 1929; Gray, 1957; Cameron, 1981). The species in this study are of similar size, closely related, do not span the 100- to 650-fold size range of other studies (Greenaway, 1984), and thus provide meaningful comparisons. The activity and terrestriality differences among the *Uca* examined here are more subtle but still distinct. *Uca subcylindrica* lives in the most elevated and arid habitats and most distant from water. *Uca panacea* prefers the periphery of sandy wind tidal flats, and often lacks water in the burrow (Powers, 1975) but is more closely tied to the water than *U. subcylindrica*. The others, *U. longisignalis* and *U. rapax,* are found in the intertidal zone and nearly always have water in their burrows.

It is generally accepted that of the epithelial types in brachyuran crab gills the thinner is the site for respiratory gas exchange while the thicker is the site of active ion transport (Copeland and Fitzjarrell, 1968; Aldridge and Cameron, 1982; Barra *et al.,* 1983). The gills as the site of exchange of gases, ions, and water are of interest to aspects of osmoregulation and desiccation tolerance in fiddler crabs of semi-arid habitats. Reduced gill surface area would be advantageous in reducing the loss of water by transpiration. On the other hand, this reduced area without a concomitant increase in thick epithelia may be a disadvantage to *Uca subcylindrica* from the standpoint of osmotic and ionic regulation. Based on an ecological series of gammaridean amphipods, Moore and Taylor (1984) predicted that an increase in gill area may be promoted in reduced salinities as a means of facilitating ion uptake. The lesser range of salinity tolerance and decreased osmoregulatory ability in *U. subcylindrica* in long-term salinity experiments may be related to the observed differences in gill morphometry.

Part of the respiratory function in terrestrial crabs is taken on by the branchial chamber lining (*e.g.*, Greenaway and Taylor, 1976; Díaz and Rodríguez, 1977). Among

fiddler crabs, *Uca subcylindrica* has the greatest branchial chamber volume, which lends to its distinctive shape and its name. There is no obvious elaboration of its surface area or vascularization, however, so it is not clear whether this is of any great adaptive significance. The egg mass volume of *U. subcylindrica* is twice that of any other *Uca* (Rabalais and Gore, 1985), and the function of the enlarged branchial chamber may be to accommodate this egg mass prior to deposition.

In summary, some of the physiological responses and gill morphometric differences among the four species of *Uca* examined are consistent with their distribution patterns and some are not. *Uca subcylindrica* inhabits by far the driest habitat and the one most subject to salinity extremes, but its osmoregulatory ability was not greater than that of *U. longisignalis*. On the other hand, *U. subcylindrica* was more tolerant of desiccation. This was paralleled by a reduced gill surface area which probably helps to reduce evaporative water loss. The ability to withstand a greater loss of body water would be advantageous to any intertidal organism subjected to periodic exposure. These factors, coupled with a more supratidal or nontidal existence in a semi-arid climate, would be of particular importance to *U. subcylindrica*. That the other species of *Uca* are potentially capable, physiologically, of tolerating many of the conditions that *U. subcylindrica* faces in its peculiar habitat suggests that factors additional to physiological abilities determine their non-overlapping distribution patterns. Primary among these are size, behavior, reproductive biology, life history patterns, dispersal, and characteristics of the early life history stages (Rabalais, 1983; Rabalais and Cameron, 1983; Rabalais and Cameron, 1985).

ACKNOWLEDGMENTS

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